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BOTANICAL GAZETTE

AUGUST 1910

THE MORPHOLOGY OF THE PODOCARPINEAE
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 138

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(WITH PLATES IV-VI)

Previous to 1902 the morphology of the Podocarpineae was an unknown field, but recently, through the contributions of COKER (5), JEFFREY and CHRYSLER (7), BURLINGAME (2), BROOKS and STILES (1), and YOUNG (25) on *Podocarpus* and *Dacrydium*, and NORÉN (11), STILES (15), THOMPSON (16, 17, 18), and TISON (22) on *Saxegothaea* and *Microcachrys*, the group as a whole has become fairly well known. *Pherosphaera*, with two species, is the the only genus as yet untouched, and therefore will not be considered in the following discussion.

One of the chief interests of the family is the question of relationships. The division of the Coniferales into the two families Taxaceae and Pinaceae was made originally on the basis of external characters, but with increasing knowledge of the Podocarpineae certain resemblances to the Araucarineae have been more and more emphasized, until it has even been suggested that these two tribes should form a group by themselves.

Three papers on *Phyllocladus* by Miss ROBERTSON (13) and Miss KILDAHL (8, 9) are of particular interest because of the difference of opinion in regard to the affinities of that genus. *Phyllocladus* was classed with the Podocarpineae by STRASBURGER, removed to the Taxineae by ENGLER and PRANTL, and finally made a sub-family by itself by PILGER (12) in 1906; and now, as its life history is studied, its place is again called in question. MISS ROBERTSON's work was

chiefly anatomical. Miss KILDAHL'S work was done in this laboratory, and I have had the opportunity of examining her preparations. The receipt of additional material has made it possible to continue the study and to fill in some of the missing stages. This work, a previous study of *Dacrydium*, and the opportunity of examining some material of *Podocarpus* have given occasion for the present paper. I shall first consider *Phyllocladus*, and later take up the larger question of the relationships of the Podocarpineae.

I. *Phyllocladus*

The material sent by Dr. L. COCKAYNE of Christchurch, New Zealand, consisted of staminate cones collected at intervals of a few days from October 16 to November 13, and ovulate cones of November 8, 13, 25, December 3, 18, 31, January 8, 28. The iron-alum hematoxylin and orange combination was found very satisfactory in staining, as it brought out cytological details remarkably well for tissues killed in formalin and alcohol.

THE MALE GAMETOPHYTE

Miss KILDAHL reports (1) the formation of two prothallial cells, the first of which is usually evanescent; (2) the presence of four, occasionally five, free nuclei in the mature pollen grain; and (3) the division of the body cell into two equal male cells.

My material furnishes a close series, beginning with the microspore stage. The wings are comparatively small and irregular, recalling those of *Microcachrys*, and are formed in the ordinary way as cavities in the exine. The intine is usually rather thin. Very small starch grains occur, but are never conspicuous. Figs. 1-5 show the cutting off of the prothallial cells. The first usually degenerates so quickly that it is hard to find in the older grains. In fig. 4 it is seen partly covered by exine; this is an oblique section escaping the wings and making the spore coats appear unusually thick.

The generative cell is formed in the usual way and divides antiparallelly, as in the case of *Ginkgo*, *Podocarpus*, and *Dacrydium*, and presumably in all the Podocarpineae. The four-celled stage, as shown in fig. 7, but for the wings might very easily be mistaken for the shedding stage in *Ginkgo*. In the latter, it will be remembered,

the generative cell does not divide until after the tube begins to grow. The spindle in *Phyllocladus* is always more or less oblique, and results in the formation of a larger, more centrally placed body cell and a small stalk cell.

In fig. 13 there is shown a peculiar but very common feature of the sections, the appearance as of an additional cell cut off from the body cell, but without a nucleus. This was noticed also in *Podocarpus* and *Dacrydium*. JEFFREY and CHRYSLER (7), in the case of *Podocarpus ferruginea* and *P. dacrydioides*, describe a second lateral derivative cell and picture it with a nucleus. BROOKS and STILES (1) find the same thing in *P. spinulosa*, but it is not clear whether a nucleus is present or not. It is in these species that the most extensive prothallial tissue is found, consisting of eight cells. In the forms studied by BURLINGAME and myself, as well as in *Dacrydium* and *Phyllocladus*, no nucleus ever appears in the extra section of cytoplasm. The explanation is most easily found in *Phyllocladus*, where horizontal sections show that it is really only a part of the stalk cell. When we consider the shape of the generative cell and the position of the spindle in the division, it is evident that an oblique wall in such a dome-shaped structure could not help resulting in the partial encircling of one cell by the other. The situation can be most clearly shown by diagrams. A horizontal section in the position shown by the dotted line *xy* in fig. 15 would give a view such as is outlined in fig. 16, while fig. 15 is the vertical section through the dotted line in fig. 16. Fig. 17 is an oblique section in about the position of the dotted line *vw* in fig. 15. In this case the second prothallial cell is seen encircled by the stalk cell. A change of focus brings into view the body and tube nuclei and a portion of one wing.

If the stalk nucleus, as shown in fig. 16, were a little more elongated, it would be quite possible to obtain a vertical section in such a position as to show a small part of it on each side of the body cell. The appearance of JEFFREY and CHRYSLER'S and of BROOKS and STILES'S figures of *Podocarpus ferruginea*, *P. dacrydioides*, and *P. spinulosa* suggests this as a possible explanation of the second lateral derivative.

The fact has been noted that the division of the generative cell is anticlinal in Podocarpineae and *Phyllocladus*, and periclinal in other conifers and in cycads, the relative position in the latter having given

rise to the term "stalk cell." It will be remembered that the division takes place in the former before and in the latter after germination has begun. Fig. 18 is a diagram showing this stage in *Dioon*, taken from CHAMBERLAIN (3). If in the case of *Phyllocladus* the generative cell should enlarge upward toward the tube before the division, we can easily see that the oblique wall, failing to touch the prothallial cell, would give us the *Dioon* situation. On the other hand, if the wall in *Dioon* were a little lower down or slightly more oblique, we should have a section very like that of *Phyllocladus*. From this point of view the distinction between the anticlinal and periclinal division appears to be related to the time at which the division takes place, and to be of little significance in itself.

Throughout the development of the gametophyte, though distinct cells are formed, each bounded by a *Hautschicht*, there is no evidence of cellulose walls. This I believe to be true also in the *Dacrydium* and *Podocarpus* which I have examined. NORÉN (11) fails to find cellulose walls in the case of *Saxegothaea* except in the first prothallial cell, and THOMPSON (17) finds them in *Microcachrys* only in the prothallial cells.

Miss KILDAHL mentions the occasional persistence of the first prothallial cell. Figs. 11 and 12 show not only this but also a still more rare case in which the second has divided. This, it will be remembered, is the usual condition in *Dacrydium*, *Microcachrys*, and *Saxegothaea*. In *Dacrydium*, moreover, the first prothallial cell very often degenerates early, which makes the resemblance to *Phyllocladus* still stronger.

As in all the Podocarpineae so far studied, the prothallial and stalk nuclei become free in the general cytoplasm. This may occur in *Phyllocladus* before the grains are shed, but sometimes not until after they reach the micropyle. The mature grain contains the body cell, and the free prothallial, stalk, and tube nuclei.

Young tubes were found in the nucellus November 20. Fig. 19 shows the tube nucleus in advance, followed by the others, and the distinctly organized body cell still in the grain.

My work does not confirm Miss KILDAHL's in regard to the male cells, as in every case where a complete series of sections was secured, a decided difference in size was evident. The functional

cell is almost always in advance. It has not only more cytoplasm than the other, but nearly always a larger nucleus, and often the other shows signs of degeneration. Figs. 20 and 32 are both drawn so as to show the largest diameter of each male cell and nucleus. The division of the cytoplasm is sometimes hard to demonstrate, and the appearance is that of two free nuclei. Careful staining, however, shows that two definite male cells are formed.

THE FEMALE GAMETOPHYTE

Some belated cones collected November 18 gave the earliest stages. Fig. 21 shows an ovule with its free nucellus, its wide open micropyle with pollen grains, and the arillus making its appearance as a slight swelling at the base. The stony part of the integument develops from a layer two cells deep. The "outer fleshy layer" does not thicken up, but remains represented by only the epidermis and the cells directly under it.

The megasporangium mother cell evidently gives rise to a row of three cells, the innermost being the functional megasporangium; in fig. 3 it has germinated and has two free nuclei. The young prothallus is surrounded by a layer of glandular, vacuolate cells encroaching on the surrounding nucellar tissue. This "spongy layer" at a later period is much more marked and the cells become binucleate. The megasporangium membrane soon appears and is well marked in the early free-nucleate stages. In having the megasporangium membrane and spongy layer *Phyllocladus* agrees with all the Podocarpineae except *Podocarpus*, and differs from all the Taxineae.

Wall formation was not found, nor archegonium initials. The development of the young gametophyte is evidently rapid, for material collected November 25 was in the free-nucleate stage, while that of December 3 contained archegonia and an occasional very young embryo.

The gametophyte produces two archegonia, each with its jacket of multinucleate cells; Miss KILDAHL found occasionally three or four. The youngest archegonium obtained is shown in fig. 24. The width at the top seems to be due to the rapid centrifugal growth of the tissues at the upper (archegonial) end of the prothallus, which is indicated by radial lines of cells and numerous spindles. The initial

has divided, forming a central cell and a primary neck cell; the latter gives rise by two divisions to a plate of four cells (figs. 25-27). An exceptional case is seen in fig. 29, where a division has occurred in each of the four cells. Cellulose walls (in this division), however, are not formed, the cells being separated merely by a *Hautschicht*, and in one of them not even a *Hautschicht* appears. The cytoplasm of the central cell is very delicate in the early stages, but gradually thickens up. The nucleus is rather small and lies at the upper end close under the neck.

There is an interesting peculiarity in the neck development of *Phyllocladus* which, so far as I know, has not been reported in any other genus. Miss KILDAHL described the pollen tube as pushing its way into the archegonium with two apparently detached cells in front of it, which she thought were the remains of a crushed neck. Fig. 32 shows this stage, but there are four neck cells, and they are connected with the adjacent jacket cells by a distinct membrane. This membrane at first sight is easily mistaken for the wall of the pollen tube, but the latter is very thin and usually shrinks away from the archegonium in the preparations.

The origin of this peculiar condition is found in a series of earlier stages. The young archegonia are superficial and the necks are covered by the heavy megasporangium membrane (figs. 24-26). The pollen tubes at this time come in contact with the prothallus near the necks, and the adjacent tissues grow rapidly, leaving the archegonia at the bottom of considerable cavities which are occupied by the tubes (fig. 36). In *Cephalotaxus*, according to COKER (4), the archegonia, in the absence of pollination, may be entirely inclosed by the growth of the lateral tissue. The megasporangium membrane is always a little thinner at the micropylar end, but disappears entirely inside the archegonial cavities (fig. 37), apparently digested by the male gametophyte. Fig. 27 shows it beginning to disappear under the advancing tube. The growth of the female tissues and the pressure of the tube result in a lateral stretching, first of the neck, then of the adjoining jacket cells (fig. 28). The walls of these latter are able to resist the digestive action and enlarge enormously, until just before fertilization they appear as the membrane mentioned above (figs. 33-35).

An interesting situation is shown in fig. 34. The ovule contained

three archegonia, of which the two shown had apparently arisen from adjacent initials and formed a complex with a common jacket. The necks, consisting of four cells each, are attached to one another, one on each side of the common wall. This wall is almost parallel with the plane of the page and passes between the two egg nuclei. In another gametophyte three archegonia were found with a single jacket layer separating two of them; the usual amount of tissue lay between them and the third.

Fig. 33 illustrates the resistance of the jacket membrane to the action of the tube. The neck of this archegonium has been pushed into a vertical position, and part of the egg cytoplasm has been squeezed away from the rest and shows signs of degeneration.

Shortly before fertilization a ventral canal nucleus is cut off, but there is no trace of a wall (figs. 30, 34). In this *Phyllocladus* agrees with *Podocarpus*, *Taxus*, and *Cephalotaxus*, but not with *Torreya*. In the latter not even a nucleus has been found.

Podocarpus is the only member of its tribe whose female gametophyte has been studied. In it COKER (5) found six to ten archegonia. The neck varies greatly, having commonly three tiers of four cells each, but sometimes the number of cells is more than twenty-five.

FERTILIZATION AND THE EMBRYO

At the time of fertilization both egg and jacket cells are rich in "proteid vacuoles," and the egg nucleus is surrounded by a homogeneous and very dense layer of cytoplasm. The contents of the pollen tube enter the egg through the neck, leaving the cells intact. Fig. 35 shows both male cells in the egg; the larger fuses with the egg nucleus, some of the cytoplasm apparently contributing to the embryo. Though no trace of the prothallial, stalk, and tube nuclei could be found in this case, it is reasonable to suppose that they entered with the rest of the contents of the tube. In fig. 27 a tube is seen pressing against the side of an archegonium. With further growth probably the wall will be forced into a vertical position, in which case fertilization can take place in the usual way.

Miss KILDAHL reports the formation of at least eight free nuclei in the proembryo, and my material furnishes nothing more. Ovules collected in January had embryos with two cotyledons and long

suspensors. The entire endosperm tissue is multinucleate, a condition which begins to appear while the archegonia are young; it results from the failure of walls to form. In the older endosperm as many as eight nuclei occur in a cell. The megasporangium at the fertilization period is about $2.5\ \mu$ thick at the lower part of the prothallus, and about $4.5\ \mu$ when the cotyledons appear (fig. 31).

Before discussing relationships, it will be helpful to summarize the important facts about *Phyllocladus*, including the work of Miss ROBERTSON and Miss KILDAHL.

SUMMARY

1. The stamen bears two abaxial sporangia.
2. The pollen grains have two wings.
3. In the male gametophyte there are two prothallial cells; the first usually disappears, the second occasionally divides.
4. The generative cell divides anticlinally but obliquely, and the stalk cell partially encircles the second prothallial and body cells.
5. The mature pollen grain contains the body cell and the free stalk, prothallial, and tube nuclei.
6. There are two unequal male cells, only the larger of which functions.
7. The ovulate structure is a strobilus with a single erect ovule in the axil of each scale.
8. A symmetrical arillus originates from the base of the ovule and remains free from the integument.
9. The outer fleshy layer is represented by two layers of cells.
10. The nucellus is free to the base.
11. The megasporangium gives rise to a row of three cells, the innermost of which is the functioning megasporangium.
12. The spongy layer and megasporangium membrane are strongly developed.
13. Each ovule contains two archegonia, occasionally three or four, each with its own jacket, but sometimes there is a complex of two in a common jacket.
14. The neck of the archegonium consists of four cells in a plate; occasionally these divide anticlinally.
15. There is a ventral canal nucleus.

16. The mature archegonium is very wide at the top and is covered by a membrane formed from the walls of the adjacent jacket cells.

17. In fertilization the contents of the pollen tube pass through the neck, leaving it intact.

18. Some male cytoplasm contributes to the embryo.

19. There are at least eight free nuclei in the proembryo.

20. The embryo has two cotyledons and a very long suspensor.

21. Mesarch bundles occur in the cladodes.

22. Taxinean sculpturing is found in the tracheids.

23. No vascular strands enter the ovule; the ovular supply consists of two strands facing each other and ending in a tracheal plate below the integument.

DISCUSSION

The characters which point toward the affinity of *Phyllocladus* with the Taxineae are: (1) the structure of the ovule, (2) the symmetrical arillus, (3) resemblances of the ovulate cone to that of *Cephalotaxus*, (4) mesarch bundles, and (5) taxinean sculpturing of tracheids. Characters indicating a relationship with the Podocarpineae are: (1) the character of the male gametophyte, (2) the structure of the stamen, (3) winged pollen grains, (4) megaspore membrane and spongy tissue.

The first point is perhaps the strongest argument for taxad affinity, as the erect, free, axillary ovule is characteristic of the whole group. This ovule, however, is a primitive type which we would expect to find at the base of any line. Though the progress of the podocarps has been toward inversion and fusion of parts, which finds its highest expression in *Podocarpus* itself, we find many relatively primitive stages represented. In *Dacrydium*, *Saxegothaea*, and *Microcachrys* the ovule is free from the scale and epimatium, except at the base, and in the various species of *Dacrydium* we find all positions from erect to completely inverted. The young ovule of *Saxegothaea* is in early stages perpendicular to the scale and becomes inverted only as the result of later growth. This, together with its position near the base of the scale, is suggestive of ancestors with erect, axillary ovules.

The homology of the symmetrical arillus which originates from

the base of the ovule, and of the one-sided epimatium arising from the scale is uncertain. The origin of the latter may be related, however, to the foliar origin of the ovules, and, as Miss ROBERTSON states, "the asymmetry is correlated with the inverted position of the ovule, so that it will not do to lay too much stress on this point, as proving that epimatium and arillus are not homologous."

Though the external resemblance between the cones of *Phyllocladus* and *Cephalotaxus* is rather striking and the vascular supply is the same, this may merely point back to a common origin of all the Taxineae. *Cephalotaxus*, moreover, has two ovules in the axil of each bract, while *Phyllocladus* agrees with the Podocarpineae in having only one.

The presence of mesarch wood in the cladodes owes its significance to the fact that mesarch wood is more common in Taxineae than in any other group of conifers. This, too, is an ancestral character, for which we would look in the primitive members of any group. STILES finds it in the ovular supply in *Saxegothaea*, whose cone is regarded as the most primitive of the podocarps.

Taxinean sculpturing of tracheids, too, would be more significant if it were confined to Taxineae, but this is by no means true. Such characters as these last two are valuable in connection with other evidence, but have little weight in themselves.

The most convincing evidence of podocarp affinity lies in the entire behavior of the male gametophyte: the formation of prothallial tissue, the freeing of the nuclei, and the early division of the generative cell. The presence or absence of prothallial cells is a definite group character; where they occur at all they are characteristic of an entire family, and where absent in one member they are lacking in all. Permanent prothallial cells are known nowhere in conifers except in Podocarpineae and Araucarineae; and the early division of the generative cell, which characterizes the former, occurs nowhere else except perhaps in araucarians. Prothallial tissue is a primitive character, possessed, as we presume, by the ancestors of all conifers; but the Taxineae have eliminated it entirely, while it still remains one of the most characteristic features of the Podocarpineae.

The morphology of the different forms of stamen in the conifers is an open question. The Taxineae, according to COULTER and

LAND (6), are reducing the epaulette type of *Taxus*, while no other family, except araucarians, has a stamen with more than two pollen sacs. If the two types have a common origin, only the *Taxus* stamen can be the primitive one; and in this case *Phyllocladus* has gone a long way in the podocarp line of development. A different origin, of course, would remove *Phyllocladus* still farther from Taxineae.

Winged pollen is entirely absent among the Taxineae, but is characteristic of the Podocarpineae, being absent only in the *Saxegothaea*. The irregularity in size and number of the wings in *Microcachrys* has given rise to THOMPSON'S (16, 17) theory that the two-winged condition has developed within the group and shows no relation to Abietineae. This gives us another podocarp line along which *Phyllocladus* has advanced.

THOMPSON (20) lays a good deal of stress on the megaspore membrane as a primitive character. It is entirely eliminated in Taxineae, but characterizes all the members of the other family except *Podocarpus* itself. As the ovulate structures of the type genus are by far the most specialized of the family, this is not surprising. Miss ROBERTSON thought the megaspore membrane and spongy tissue were in some way correlated with the presence of winged pollen, but their occurrence in *Saxegothaea* with its wingless microspores breaks down this supposition.

CONCLUSION

When we consider the question of relationships, it is evident on the whole that: (1) *Phyllocladus* has primitive characters of the Taxineae which are being eliminated in the Podocarpineae; (2) it has primitive characters of the Podocarpineae which have been entirely eliminated in the Taxineae; (3) it has some advanced characters of Podocarpineae; (4) the taxad resemblances are on the whole more superficial and variable, and the podocarp features more fundamental; (5) the resemblances to Podocarpineae are too strong to justify the retention of the intermediate family.

We conclude, therefore, that *Phyllocladus* is a relatively primitive member of the Podocarpineae, which branched off from them a comparatively short time after their separation from Taxineae. Whether the two families form a distinct line from other conifers is not at all involved in this conclusion.

II. Podocarpineae and Araucarineae

The more important contrasts between the araucarian and podocarp lines are in the structure of the stamen and ovulate strobilus, and in the method of fertilization. The araucarian stamen is a comparatively primitive type and is somewhat suggestive of *Ginkgo*. It is one-sided and bears three to thirty pendent pollen sacs; while all the genera of the Podocarpineae, as before mentioned, have the microsporangia definitely reduced to two.

The ovulate cone in Araucarineae is a compact structure with many scales, ripening dry; while the podocarp line is characterized by the reduction in the number and size of cone scales and the tendency to fleshy development. *Saxegothaea*, the form which stands nearest the araucarians, shows the least amount of reduction in both size and number of scales; *Microcachrys* is next; while in other forms the cone is represented by the single, apparently terminal, ovule and a few rudimentary scales. The podocarp ovules have the arillus, or epimatium, which is absent in araucarians. The cone scale of *Araucaria*, on the other hand, bears the so-called ligule, represented in *Agathis* by only a slight projection from the surface. The ovules of *Saxegothaea* are united with the scale only at the base, while in *Araucaria* they are described as imbedded in the tissues of the scale. In *Agathis*, however, the ovules are free and the seeds winged.

The female gametophyte is too little known in either group for any adequate comparison. That of the Araucarineae, however, is apparently much more primitive than that of the known podocarps. The archegonia are very numerous and are described (SEWARD and FORD 14) as situated at the bottom of deep pits and usually not connected with the surface by necks. Investigation is needed here to show whether they are really hypodermal, or whether the condition is brought about by overgrowth of adjacent tissue in the development of a neck so massive as not to have been recognized. The position of the ovule of Araucarineae in the tissues of the scale is another subject which needs interpretation.

Fertilization in Araucarineae (THOMPSON 19) is angiosperm-like, in that the pollen does not reach the ovule, the tubes growing over the surface of the scales to reach the micropyle.

The first suggestion of relationship between the two groups came from the study of the male gametophyte. This has recently been supplemented by studies of *Saxegothaea*, which have brought out striking resemblances to certain species of araucarians. The geographic distribution is also suggestive of alliance between these two great southern groups.

THE MALE GAMETOPHYTE

In the Araucarineae, as in the Podocarpineae, there are two original prothallial cells, from which by subsequent divisions a more or less extensive tissue is formed. In Araucarineae there may be as many as thirty cells (LOPRIORE 10; THOMPSON 21). JEFFREY and CHRYSLER (7) found an apparently mature pollen grain of *Agathis australis* with a prothallial complex of eight cells, which is the situation in some species of *Podocarpus*. Other species of *Podocarpus* have four cells, resulting from a single division of each original prothallial cell. In *Dacrydium*, *Saxegothaea*, and *Microcachrys* there are two to four permanent prothallial cells, in *Phyllocladus* one to three. Thus we have a complete overlapping prothallial reduction series from *Agathis* to *Phyllocladus*.

The generative cell is found in Araucarineae as in the others, but the division into stalk and body cell has not been observed. Unless this division takes place in the tube, as is true of most conifers, it must either have been eliminated or missed in the preparations. The otherwise close correspondence with the gametophyte of Podocarpineae inclines one toward the latter supposition. Further work is needed on this point.

THE OVULE AND FEMALE GAMETOPHYTE

The single inverted ovule is characteristic of both families. The inversion was probably developed independently, however, in the two lines. In *Saxegothaea*, as has been said before, the young ovule changes from an erect to an inverted position in the course of its development. The free nucellus of *Dacrydium* and *Phyllocladus* is a primitive feature which they have in common with araucarians.

The female gametophyte, as before stated, is little known. A

point of resemblance, however, between Araucarineae, *Phyllocladus*, and *Podocarpus* is found in the cutting off of the ventral canal nucleus in the archegonium.

SAXEGOTHAEA

The resemblance of *Saxegothaea* to the araucarians, noted by STILES (15), NORÉN (11), THOMPSON (18), and TISON (22), consists chiefly of anatomical characters and certain external features of the cones. STILES finds in the stem tracheids somewhat araucarian in character, "an occasional tendency to a two-ranked arrangement of the pits, and in these cases the pits become alternate and hexagonal." Two-ranked and alternate pits horizontally flattened have also been found in *Dacrydium*. The prominence of transfusion tissue is another character suggestive of araucarian affinity.

The staminate cone is described by STILES as somewhat araucarian in general appearance, and the wall of the microsporangium as strikingly like that of *Araucaria Rulei*. BROOKS and STILES (1), in their study of *Podocarpus spinulosa*, state that the wall of the sporangium is very like that of *Saxegothaea* and *Araucaria*. Wingless pollen is another point of contact. The fact that the pollen grains of all the other Podocarpineae have wings does not affect the argument, if we accept THOMPSON's theory that they were developed within the group (15, 16).

In the ovulate cones of both *Saxegothaea* and *Araucaria*, especially *A. Rulei*, there is a gradual transition from foliage leaves to sporophylls. This and the similarity in the vascular anatomy are considered by THOMPSON and TISON as indications of the simple nature of the strobilus in these groups. The occurrence of a single resin duct in the sporophyll is, according to STILES, another indication of this in *Saxegothaea*.

One of the most striking features of *Saxegothaea* is the projection of the nucellar tissue through the micropyle, where it expands to form a stigma-like knob. The same thing occurs less conspicuously in Araucarineae, but, with the exception of a few abnormal cases in angiosperms, is elsewhere unknown. This feature appears to be related physiologically to the difficulty of fertilization, and its morphological significance is doubtful. THOMPSON (19) sees in it a

tendency toward protosiphonogamic fertilization, significant in relating *Saxegothaea* to the araucarians.

A good deal of stress has been laid recently on the distribution of the vascular bundles in the ovulate sporophylls. STILES finds the branching in *Saxegothaea* very similar in the main to *Araucaria Rulei* and *A. Cookei*, and the arrangement in *Microcachrys*, though not unlike that of *Saxegothaea*, resembles more closely *A. Bidwillii*. TISON agrees essentially with STILES in regard to the details in *Saxegothaea*, but finds greater resemblance to *A. brasiliiana* and *A. imbricata*.

RESULTS

STILES, NORÉN, THOMPSON, and TISON all agree in the relationship of the two groups, the intermediate position of *Saxegothaea*, and the simple structure of the ovulate scale in the two families, but they differ somewhat in the application of their results. STILES says: "While we must wait for fuller knowledge before making any definite statement, it would appear that these two orders of Coniferales are descended from some common ancestor with its micro- and megasporophylls both arranged spirally in cones. Along one line of descent we find the Araucarieae, along the other is *Saxegothaea* leading on to *Microcachrys* and the other Podocarpeae." NORÉN comes to the same conclusion, regarding *Saxegothaea* as nearest to the Araucarineae, but unquestionably a member of the Podocarpineae; but TISON considers it more closely related to the latter group, and regards *Microcachrys* as the connecting link.

But it is the attempt to homologize the ovulate structures of conifers that has given rise to the greatest amount of discussion. In conifers with foliar ovules, as is well known, there is more or less completely represented a double system of bundles, that from which the ovule gets its supply being inverse to the other. The two systems may originate separately from the axis, or the one supplying the ovule may arise at various situations from the other. The former varies also in extent, from a considerably branched system to one or two weakly differentiated bundles.

WORSDELL (23) in 1899 made a study of the distribution of the vascular bundles in various conifers, and in 1900 (24) published a

very complete historical account of the controversy on the morphology of the ovulate cone. He agrees with CELAKOVSKY that the arillus of Taxaceae, the ligule of *Araucaria*, and the ovuliferous scale of the other Pinaceae are homologous and are all a second integument, that all the ovulate cones are morphologically compound, but that the sporophyll is suppressed and represented by the ovule alone.

THOMPSON (18) in 1909 brought out some interesting data in regard to the inversion and its relation to the theory of the axillary shoot. The inversion of the bundles supplying the ovule he explains as normal for sporangial supply, and cites cases of such inversion in the microsporophylls of cycads and of some conifers. In *Tsuga* he found two inversions, the ovular supply being inverse to that of the scale, which in turn is inverse to that of the bract. The first inversion he considers as homologous with that of the scale of *Saxegothaea* and related to the ovule, while the second may be explained by the theory of the compound nature of the sporophyll. On this basis he makes two groups of conifers, the Araucarineae and Podocarpineae having simple strobili and ovules on the morphological upper surface of the scale, and the other Pinaceae having compound strobili and ovules morphologically abaxial.

TISON regards the arillus of *Saxegothaea* and the ligule of *Araucaria* as homologous with the ovuliferous scale of other conifers, calling them an ovuliferous appendage. He does not commit himself in regard to the axillary shoot theory as affecting Abietinae, Cupressinae, and Taxodinae, but agrees with THOMPSON that the cones of *Saxegothaea*, Podocarpineae, and Araucarineae are simple. He favors the inclusion of *Saxegothaea* and Podocarpineae in the Araucariales suggested by SEWARD and FORD (14).

CONCLUSION

After reviewing the whole situation, one is impressed with the fact that both Podocarpineae and Araucarineae are very primitive, that they are probably related, but that the question is by no means settled. The whole conifer group still appears as a maze of cross resemblances. If we confine ourselves to one or two characters, the problems of relationship are comparatively simple, but bring more into consideration, and we are immediately in trouble. The

relation of the podocarps with Araucarineae on the one hand, for instance, is complicated with evidence of connection through *Phyllocladus* with taxads on the other; and the two last-named tribes are apparently very widely separated from one another. It is true that the evidence for the first relation is the stronger, for without *Phyllocladus* the question of taxad affinity would hardly be raised at all; while without *Saxegothaea* we should still have much evidence of the other connection. The existence of *Phyllocladus*, however, cannot be disregarded.

On the other hand, the argument for araucarian connection lacks conclusiveness. In the first place, it is based largely on primitive characters. These may indicate merely that neither group has advanced far from the original ancestral conifer stock. The two lines may be quite distinct and both short. Two short branches from the same trunk may have their ends nearer together than two twigs of the same long branch. Most of the remaining evidence depends upon the external features of the cones and the distribution of vascular bundles. Such evidence is unsatisfactory on account of the great variability of the structures concerned. Great variations are found between closely related forms. *Araucaria* with its ligule and apparently imbedded ovule, and *Agathis* with its free winged seed, or the ovulate structures of different species of *Dacrydium*, are examples. TISON finds variations in the arrangement of the vascular bundles of *Saxegothaea*, not only in different individuals, but in the same plant. He says: "En ce qui concerne les écailles fertiles, je dois tout d'abord faire remarquer que la disposition du système fasciculaire à leur base, dans la région ovulifère, est très variable souvent dans un même cône, ces variantes n'étant pas nécessairement en rapport avec la position des bractées sur les cônes."

The fact of variability makes it easy to imagine the derivation of a structure from one unlike it in appearance, as the arillus and ligule or ovuliferous scale; but on the other hand, their independent origin becomes equally simple, and one is inclined to doubt the morphological need of such homologies. It may be that the conflicting lines of resemblance among conifers point to a more ancient lineage for all the families than we are apt to think, and in this case the significance of variable features becomes still less.

The greatest gap in our present knowledge of conifers is shown by the Araucarineae. Even in the male gametophyte, which supplies perhaps the strongest argument in the above discussion, a good deal of work is needed. The female gametophyte is little known and the embryo practically not at all. Beside this, we should know the early development of the ovulate strobilus for a proper understanding of the morphology of its parts. In the Podocarpineae we lack adequate knowledge of the female gametophyte, embryo, and development of ovulate structures. Until further data on these points are available, we should be hardly justified in coming to a definite decision in regard to relationships, and at present it seems best to hold Taxineae, Podocarpineae, and Araucarineae apart as separate tribes, leaving open the question of larger groupings among conifers.

Grateful acknowledgments are due to Professors J. M. COULTER and C. J. CHAMBERLAIN, under whose direction this work was done.

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EXPLANATION OF PLATES IV-VI

Zeiss compensating oculars 4 and 6 mm. and Bausch and Lomb objectives $\frac{1}{8}$, $\frac{1}{2}$, and $\frac{1}{6}$ mm. were used. All drawings, except figs. 15, 16, and 18, were made with the aid of the camera lucida. The magnifications refer to the figures as they appear on the plates, after having been reduced one-half in reproduction.

Abbreviations: *p*₁, first prothallial cell; *p*₂, second prothallial cell; *g*, generative cell; *s*, stalk cell; *b*, body cell; *t*, tube nucleus; *a*, arillus; *n*, neck; *m*₁, functioning male cell; *m*₂, functionless male cell; *vn*, ventral canal nucleus; *e*, egg nucleus; *m*, megaspore membrane; *sp*, spongy tissue.

FIG. 1.—Microspore. $\times 950$.

FIG. 2.—Spindle for the first prothallial cell. $\times 950$.

FIG. 3.—First prothallial cell cut off. $\times 950$.

FIG. 4.—Spindle for the second prothallial cell; first prothallial cell partly covered by intine. $\times 950$.

FIG. 5.—Second prothallial cell cut off, the first degenerating. $\times 950$.

FIG. 6.—Spindle for generative cell. $\times 950$.

FIG. 7.—Tube, nucleus, generative cell, and prothallial cells. $\times 950$.

FIGS. 8, 9.—Generative cell dividing. $\times 950$.

FIG. 10.—Mature pollen grain. $\times 950$.

FIGS. 11, 12.—First prothallial cell persistent and the second divided. $\times 950$.

FIG. 13.—Mature grain, showing a part of the stalk cell on each side of the body cell. $\times 950$.

FIG. 14.—Nuclei becoming free. $\times 950$.

FIG. 15.—Diagram of vertical section through dotted line in fig. 16.

FIG. 16.—Diagram of horizontal section through dotted line xy of fig. 15, showing form of stalk cell.

FIG. 17.—Horizontal section, showing stalk and second prothallial cells and tube and body nuclei. $\times 950$.

FIG. 18.—Outline drawing of *Dioon*.—From CHAMBERLAIN.

FIG. 19.—Body cell in the grain; stalk, tube, and prothallial nuclei in the tube. $\times 440$.

FIG. 20.—Body cell divided, forming two unequal male cells. $\times 440$.

FIG. 21.—Longitudinal section of ovule and bract; pollen grains on the nucellus. $\times 45$.

FIG. 22.—Young stage of the arillus; detail of fig. 21. $\times 440$.

FIG. 23.—Two-nucleate stage of female gametophyte; detail of fig. 21. $\times 440$.

FIG. 24.—Young archegonium, showing primary neck and central cells. $\times 440$.

FIG. 25.—Young archegonium; primary neck cell divided. $\times 440$.

FIG. 26.—A neck cell dividing. $\times 440$.

FIG. 27.—Four-celled neck; megasporangium membrane disappearing before advancing pollen tube; the space between the membrane and neck cells is due to shrinkage. $\times 440$.

FIG. 28.—Stretching of adjacent jacket cells under pressure of the pollen tube; body cell and central nucleus not yet divided. $\times 440$.

FIG. 29.—Eight-celled neck. $\times 440$.

FIG. 30.—Egg and ventral canal nucleus. $\times 440$.

FIG. 31.—Endosperm cells and megasporangium membrane; January 28. $\times 950$.

FIG. 32.—Egg ready for fertilization; four-celled neck and jacket membrane; male cells, stalk, prothallial, and tube nuclei. $\times 440$.

FIG. 33.—Effect of pollen tube on an archegonium; the membrane intact. $\times 440$.

FIG. 34.—Two archegonia in a common jacket; two pollen tubes. $\times 340$.

FIG. 35.—Fertilization. $\times 440$.

FIG. 36.—Female gametophyte. $\times 45$.

FIG. 37.—Megaspore membrane and archegonial cavities. $\times 440$.





